

SURFACE SCULPTURING OF THE ABDOMINAL INTEGUMENT OF MEMBRACIDAE AND OTHER AUCHENORRHYNCHA (HOMOPTERA)

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Abstract.—Scanning electron microscopic studies of the abdominal integument of auchenorrhynchous Homoptera indicate the presence of a variety of features including sensilla, acanthae, and microtrichia, the variability of which cannot be resolved by the dissecting microscope. Three classes of structures are recognized based on their cellular components: 1) multicellular processes (sensilla); 2) unicellular processes (acanthae); and 3) subcellular processes (microtrichia). Four kinds of sensilla were found: sensilla coeloconica, sensilla papillosa (previously undescribed), sensilla trichodea, and sensilla placodea. In a survey of 46 genera representing 12 families (Eurymelidae, Cicadellidae, Membracidae, Biturritiidae, Aetalionidae, Cercopidae, Aphrophoridae, Tibicinidae, Cixiidae, Delphacidae, Fulgoridae, and Flatidae), sensilla and non-sensory protuberances were found on the non-genital abdominal terga of members of all auchenorrhynchous superfamilies except the Fulgoroidea.

Key Words: Homoptera, Auchenorrhyncha, morphology, integument, surface sculpturing, sensilla

Examination of the abdominal integument of many auchenorrhynchous Homoptera by scanning electron microscopy reveals several fine-structural features of potential interest to systematists. Previously, these features, which include various types of sensilla and non-sensory protuberances, have been neglected or viewed superficially as textures in revisionary works. The objectives of this paper are to describe the common fine-structural features of integument sculpturing in the Membracidae and related groups, to propose a nomenclature for such features, and to discuss their diversity and value for hypothesizing relationships among taxa.

Harris (1979) summarized the descriptive terminology of insect integumental sculpturing, proposing the use of relative rather than absolute measures of size of the

individual elements of sculpturing (e.g. punctate vs. punctulate). He further proposed the prefixing of terms for sculpturing visible only at magnifications greater than 100 \times with "micro-" (e.g. micropunctate). While such terminology is useful at the descriptive level, it can be misleading with regards to homology if the elements of the sculpturing have fine-structure themselves. For example, the terms "punctate" and "foveate" could refer to inornate depressions in the integument as well as sensillar pores. Therefore, some nomenclatural means for differentiating integument textures based on the fine structure of the individual elements is needed if homologies among such structures are to be taken into account.

The terminology used herein is derived as much as possible from the hypothesized functional and developmental aspects of the

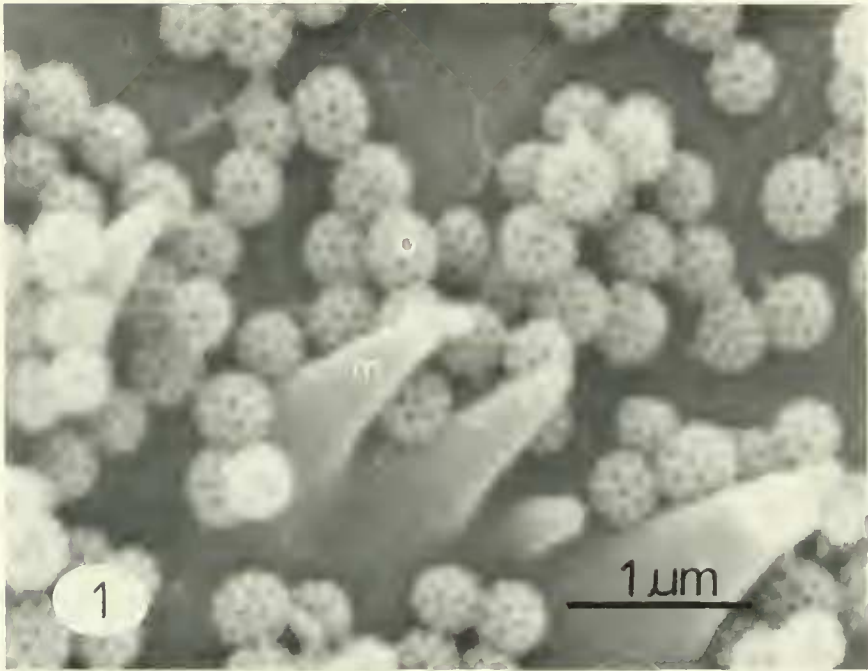


Fig. 1. Detail of abdominal integument of a cicadellid, *Draeculacephala* sp. showing microtrichia (m) and brochosomes (b).

features described following Snodgrass' (1935) classification of the cuticular features of insects as updated by Richards and Richards (1979) and Zacharuk (1985).

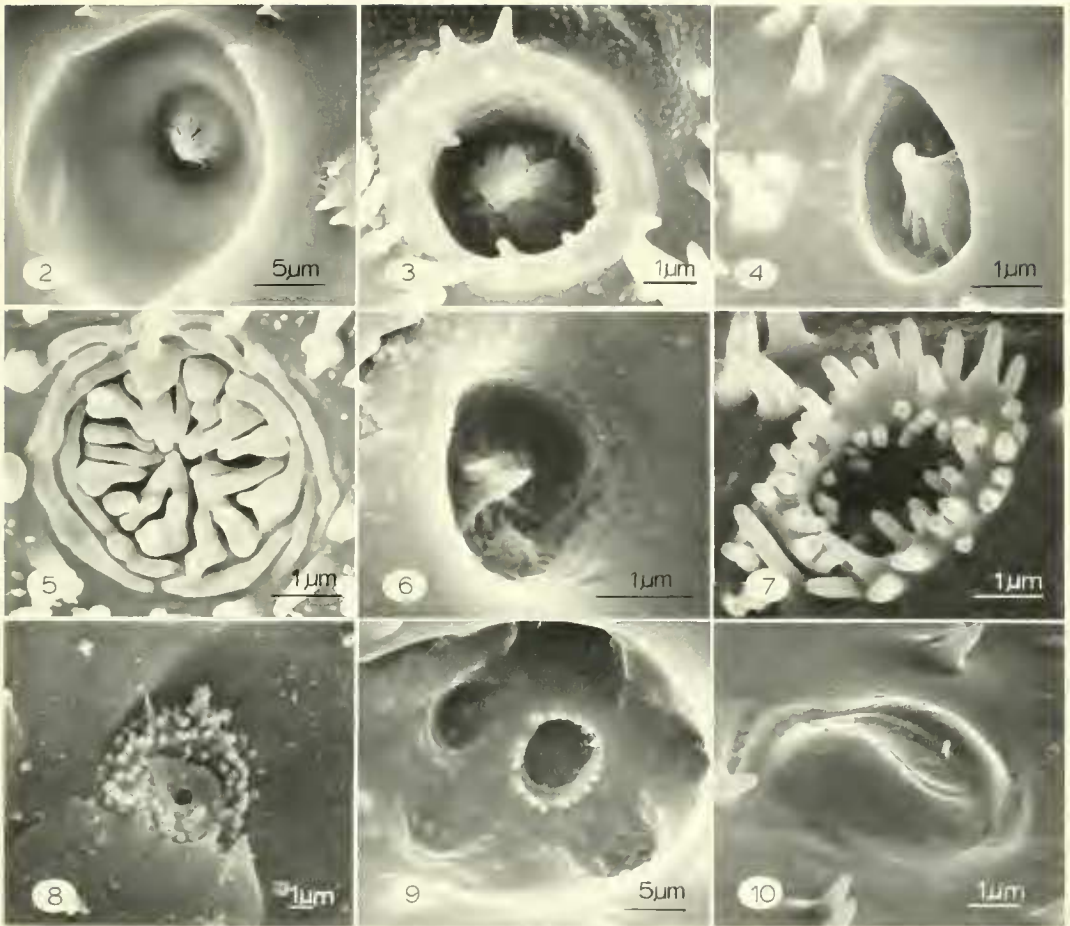
Most detailed observations of the integumental fine-structure of Auchenorrhyncha have been restricted to the mouthparts (e.g. Baekus and McLean 1983), antennae (e.g. Lewis and Marshall 1970, Bourgoïn 1985), and genitalia (e.g. Restrepo-Mejia 1980). Other observations include Wood and Morris' (1974) survey of 100 species of Membracidae for the presence of articulated hairs (sensilla trichodea) on the pronotum, Wood's (1975) observations on the ultrastructure of the membracid pronotal integument, and Kitching and Filshie's (1974) study of the anal apparatus of membracid nymphs. Smith and Littau (1960) and Günthart (1977) documented the presence of minute spherical excretory granules called brochosomes covering the bodies of some leafhoppers. Presently, such observations

have not been applied to systematic studies and the integument of body parts other than those mentioned above has been virtually ignored.

MATERIALS AND METHODS

Most of the materials examined were dried museum specimens (see Table 1 for a list of taxa examined). All are deposited in the North Carolina State University Insect Collection (Department of Entomology, North Carolina State University, Raleigh). The abdomen of each was removed, glued to an aluminum stub with conductive graphite paint, coated with gold or gold/palladium in a sputter coater and observed and photographed in a JEOL T200 or Philips 505T scanning electron microscope at 10–20 kV.

To determine whether air-drying significantly distorted the fine-structural features being examined, some specimens preserved in 70% ethanol were dehydrated in a graded



Figs. 2–10. Abdominal sensilla of auchenorrhynchous Homoptera. 2–6, Sensilla coeloconica. 2, *Enchenopa* sp. 3, *Cymbomorpha amazona*. 4, *Acutalis tartarea*. 5, *Oncometopia orbona*. 6, *Philaenus* sp. 7–9, Sensilla papillosa. 7, *Cymbomorpha amazona*. 8, *Aconophora cultellata* Walker. 9, *Hypsoprora coronata*. 10, Sensillum placodeum, *Centrodontus atlas*.

series of ethanol (80, 95, and 100%), dried in a Tousimis Samdri-PVT-3B critical point drier and coated and observed as described above. In this comparison, air-drying did not appear to significantly distort the fine-structural features observed.

Many of the cicadellids examined had the integument covered with brochosomes (Fig. 1; for a description, see Smith and Littau 1960) which obscured other features of the integument. According to Günthart (1977), these can be removed by soaking the specimens in hexane, diethyl ether, or methanol.

(Interestingly, the presence of brochosomes may itself be of taxonomic significance. They were found on several cicadellids, an eurymelid, and an actalionid, but not on any of the other specimens examined—see Table 1.)

To determine the cellular basis for the individual elements of surface sculpturing, the abdomens of two specimens preserved in 70% ethanol, one pharate and one fully-sclerotized adult, were embedded in Spurr medium (Hayat 1986), sectioned with an ultramicrotome, slide mounted, stained with

Table 1. Summary of observations on the abdominal integument of selected auchenorrhynous Homoptera. (Arrangement of higher taxa follows that of Evans (1977) except where otherwise noted.)

Taxon	Sensilla	Other Features*
Cicadelloidea		
Eurymelidae		
<i>Eurymela</i> sp.	t, c	m, b
Cicadellidae		
<i>Ledra</i> sp.	t, c	d
<i>Evacanthus</i> sp.	t, c	m, b
<i>Idiocerus</i> sp.		m, b
<i>Oncometopia</i> sp.	t, c	m
<i>Draculacephala</i> sp.	t, c	m, b
Membracoidea		
Membracidae (<i>sensu</i> Deitz 1975).		
Centrotinae		
Platycentrini		
<i>Tylocentrus</i> sp.	t	a
Nessorhininae		
Nessorhinini		
<i>Goniolomus</i> sp.	t, c	d
Membracinae		
Aconophorini		
<i>Aconophora</i> spp.	t, c, pa	d
Talipedini		
<i>Talipes appendiculata</i> (da Fonseca)	t, c	d
Hoplophorionini		
<i>Alchisme</i> sp.	t, c, pa	m
<i>Hoplophorion</i> sp.	t, c, pa	m
<i>Ochropepla</i> sp.	t, c, pa	a
<i>Platycotis vittata</i> (Fabricius)	t, c, pa	m
<i>Potnia</i> sp.	t, c, pa	d
<i>Stalotypha</i> sp.	t, c, pa	m
<i>Umbonia crassicornis</i> (Amyot & Serville)	t, c, pa	m
Membracini		
<i>Campylenchia latipes</i> (Say)	t, c	d
<i>Enchenopa</i> sp.	t, c	d
Hypsoprurini		
<i>Hypsoprora coronata</i> (Fabricius)	t, pa	a
Centrodontini		
<i>Centrodontus atlas</i> Goding	t, c, pl	m
Darninae		
Cymbomorhini		
<i>Cymbomorpha amazona</i> Stål	t, c, pa	m
Procyrtini		
<i>Procyrta</i> sp.	t, c	m

Table 1. Continued.

Taxon	Sensilla	Other Features*
Darnini		
<i>Stictopelta</i> sp.	t, c	m
Hyphinoiini		
<i>Hyphinoe</i> sp.	t, c	m
Hemikyphthini		
<i>Proterpia</i> sp.	t, c	m
Smiliinae		
Acutalini		
<i>Acutalis tartarea</i> (Say)	t, c	d
Ceresini		
<i>Spissistilus festinus</i> (Say)	t, c	m
<i>Cyphonia</i> sp.	t, c	m
Amastrini		
<i>Vanduzeeae arquata</i> (Say)	t, c	m
Smiliini		
<i>Atymna quercu</i> (Fitch)	t, c	m
<i>Archasia auriculata</i> (Fitch)	t, c	m
Tragopini		
<i>Tragopa</i> sp.	t, c	m
Polyglyptini		
<i>Entylia carinata</i> (Forster)	t, c, pa	m
<i>Polyrhysa</i> sp.	t, c, pa	m
Stegaspidae		
Microcentrini		
<i>Microcentrus caryae</i> (Fitch)	t, c	m
Heteronotinae		
Heteronotini		
<i>Heteronotus</i> sp.	t, c	m
Biturritidae (= Lampropteridae <i>sensu</i> Evans 1948)		
<i>Tropidaspis</i> sp.	t, c	d
<i>Biturritia</i> sp.	t, c	m
Aetalionidae		
<i>Aetalion reticulatum</i> (Linnaeus)	t, c	d, b
<i>Darthula hardwickii</i> (Gray)	t	d
Cercopoidea		
Cereopidae		
<i>Prosapia bicincta</i> (Say)	—	—
Aphrophoridae		
<i>Philaenus</i> sp.	t, c	m
Cicadoidea		
Tibicinidae		
<i>Tibicen</i> sp.	t, c, pl	m
Fulgoroidea		
Cixiidae		
<i>Pintalia</i> sp.	—	—

Table 1. Continued.

Taxon	Sensilla	Other Features*
Delphacidae		
<i>Liburniella ornata</i> (Stål)	—	—
Fulgoridae		
<i>Alphina glauca</i> (Metcalf)	—	—
Flatidae		
<i>Metcalfa pruinosa</i> (Say)	—	—

* KEY: a = simple acanthae; b = brochosomes; c = sensilla coeloconica; d = toothed acanthae; m = microtrichia; pa = sensilla papillosa; pl = sensilla placodea; 1 = sensilla trichodea; — = absence of above features.

methylene blue, and examined under a compound microscope.

RESULTS

Sensilla and non-sensory protuberances were found on the non-genital abdominal terga of adult representatives of all the auchenorrhynchos superfamilies except Fulgoroidea (i.e. Membracoidea, Cicadelloidea, Cercopoidea, and Cicadoidea; see Table 1).

Richards and Richards (1979) classified the cuticular protuberances of insects into four major groups based on their cellular structure: 1) multicellular undifferentiated (spines); 2) multicellular differentiated (sensilla); 3) unicellular (acanthae); and 4) subcellular (microtrichia). Three of these (2, 3, and 4) were found on the abdominal integument of membracids. They are described as follows: A. Sensilla. Four kinds of sensilla-like structures were found and are named (with one addition) according to the classifications of Snodgrass (1935) and Zacharuk (1985) based on external morphology. The following designations are necessarily tentative until the functions of these features are elucidated through ultrastructural studies.

Sensilla trichodea are socketed, hair-like structures—setae—present in varying numbers and sizes on the abdomen of many Auchenorrhyncha (e.g. Fig. 24).

Sensilla coeloconica are pegs or cones set

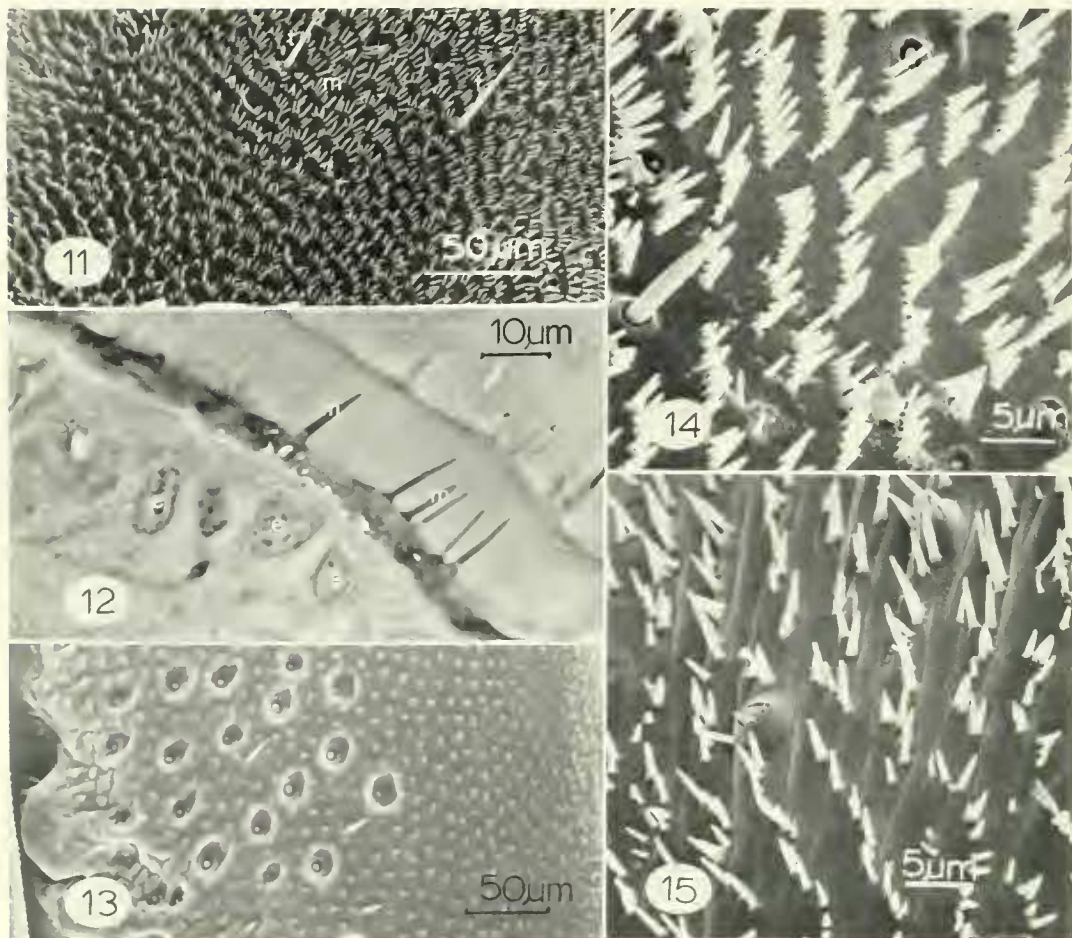
in pits approximately 1–20 μm in diameter. They vary in size, abundance, and fine-structure. When present they appear as punctations or foveae or are not visible at low magnifications (Figs. 2–6).

Sensilla placodea consist of a plate of sensory cuticle surrounded by a membranous ring 1–5 μm in diameter (Fig. 10). They were found on only two of the specimens examined (see Table 1) but eventually may be found to be common in some groups (e.g. Cicadoidea).

Sensilla papillosa are previously undescribed structures, presumed to be sensilla, consisting of groups of papillae 2–5 μm in diameter that may be associated with a pore or membrane. They are less abundant than sensilla coeloconica and are generally not visible at low magnifications (Figs. 7–9). Further study of the ultrastructure of these features is needed to determine whether they can be assigned to any of the other classes of sensilla.

B. Acanthae, microtrichia, and derivatives. The unicellular structures of Membracidae vary from single tooth-like or pectinate processes (acanthae) to divided groups of subcellular projections (microtrichia). They also vary in size and relative abundance, and give the integument a grainy to finely pubescent appearance at low magnification. Differentiation among acanthae and microtrichia presents some difficulty as it requires knowledge of the developmental origins of these structures (Richards and Richards 1979). Thin-sections of a pharate adult *Archasia auriculata* (Fitch) (Fig. 12, cf. Fig. 11) indicate that the small hair-like projections on the integument surface are relatively numerous compared to the underlying epidermal cells, demonstrating their subcellular nature. It seems likely that each of the arcuate groups of these microtrichia seen in Fig. 11 corresponds to an individual epidermal cell and is therefore derived from an acanthus (*sensu* Richards and Richards 1979).

There is often a wide range of variation in the relative amount of development of



Figs. 11–15. 11–12. Cellular structure of the cuticular protuberances of a membracid, *Archasia auriculata*. 11, Distribution of microtrichia (m) and sensilla trichodea (t) on abdominal tergum IV. 12, Thin-section through a portion of abdominal tergum integument showing positions of epidermal cells (e) relative to microtrichia. 13. A portion of abdominal tergum IV of *Enchenopa* sp. (Membracidae) illustrating variation in the integument sculpturing from anterior (left) to posterior (right). 14–15. Microtextures of membracid integument. 14, Microgranulate, *Acutalis tartarea*. 15, Microrugose, *Atymna guerci*.

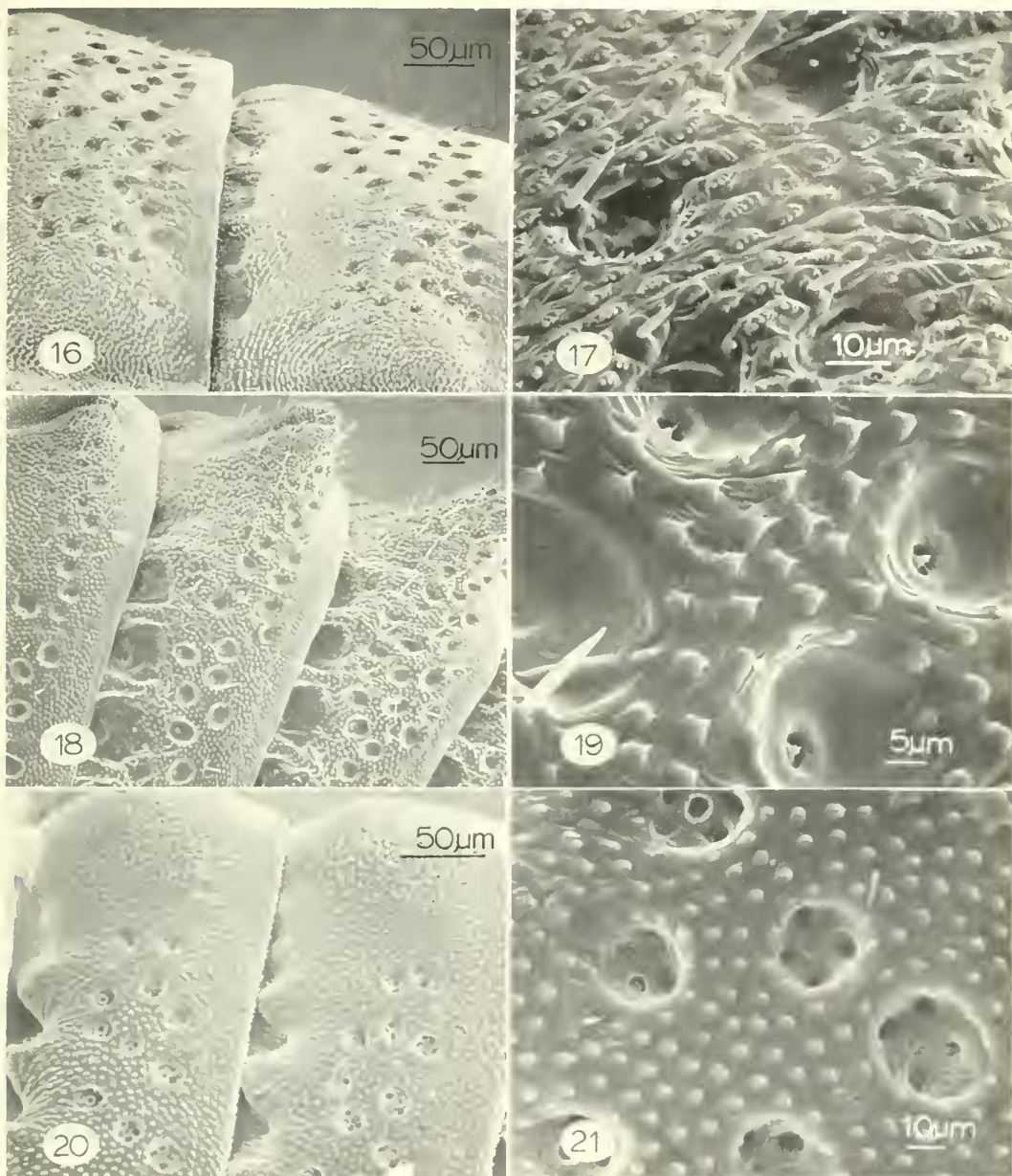
acanthae and microtrichia on individual specimens. The general trend in Membracidae is from maximal to minimal development from anterior to posterior ends of the individual terga (Fig. 13). Thus, when comparing taxa, it may be desirable to consider homologous sites on the specimens, or to compare only the maximal or minimal conditions of these structures.

Patterns of subcellular sculpturing, other than microtrichia, that are uniformly dis-

tributed over the integument surface may be referred to as "microtexture." Thus far, three conditions have been observed and are named according to the convention of Harris (1979): microglabrous (smooth, e.g. Fig. 27); microgranulate (grainy, Fig. 14); and microrugose (wrinkled, Fig. 15).

DISCUSSION

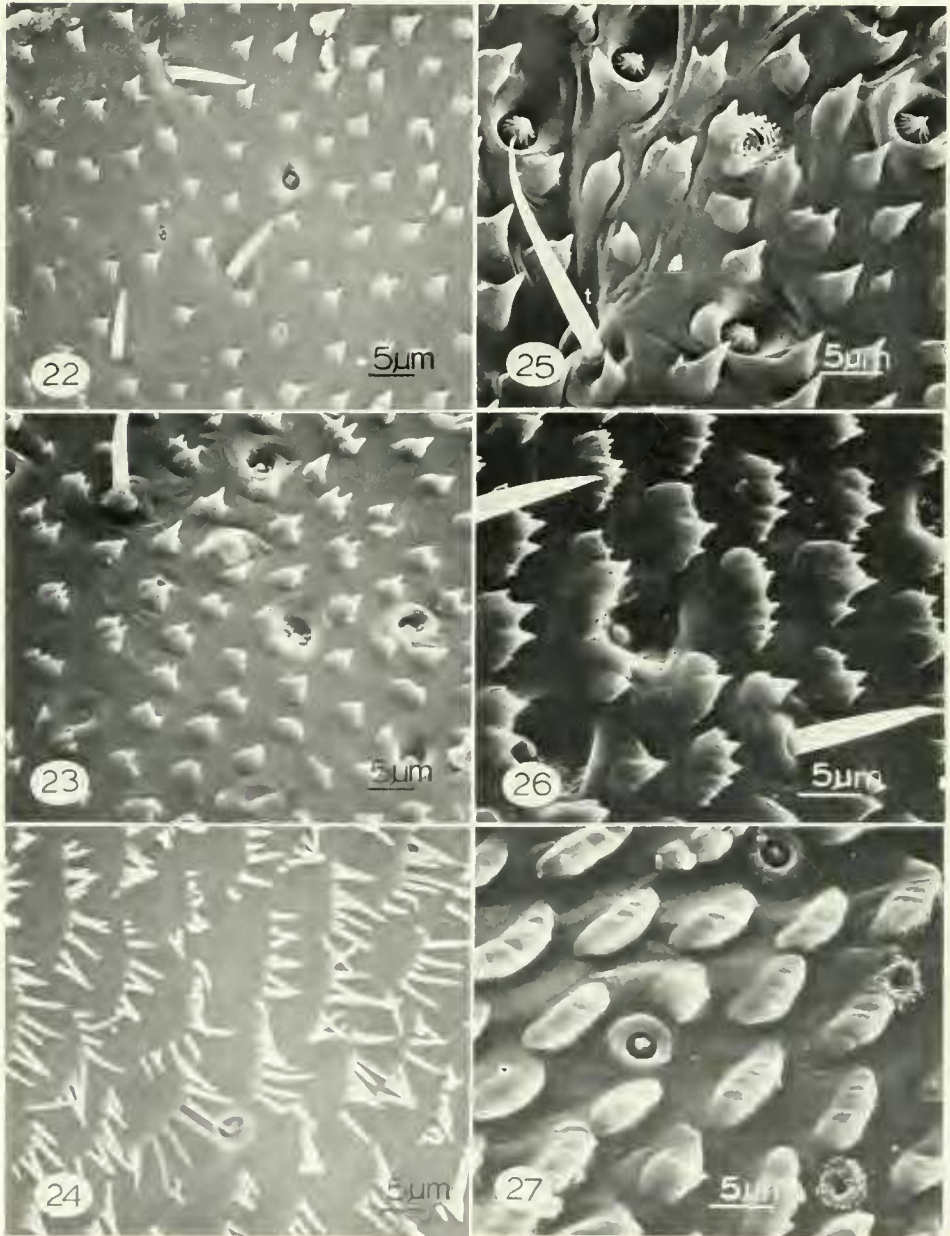
The observations documented here demonstrate the need to study the fine-structure



Figs. 16–21. Comparisons of foveae on the abdominal terga of three membracids (lateral views). 16–17, *Goniolomus tricorniger*. 16, Terga III and IV. 17, Detail, tergum IV. 18–19, *Talpes appendiculata*. 18, Terga III–V. 19, Detail, tergum IV. 20–21, *Hysoprora coronata*. 20, Terga III and IV. 21, Detail, tergum III.

of integumental sculpturing if such features are to be used in systematics. Simply characterizing integument features as textures may be misleading with regards to homologies among such characters at the level of

the individual fine-structural elements. Furthermore, examination of the integument fine-structure yields a wealth of morphological information that is potentially applicable to phylogenetic studies. These



Figs. 22–27. Variation of non-sensory protuberances on abdominal tergum IV in two membracid tribes. 22–24, Hoplophorionini. 22, *Ochropepla* sp. 23, *Potnia* sp. 24, *Alchisme* sp. 25–27, Aconophorini. 25, *Aconophora cultellata* Walker (t, sensillum trichodeum). 26, *Aconophora grisescens*. 27, *Aconophora* sp.

points are best illustrated with examples from the membracid taxa surveyed.

The species *Goniolomus tricorniger* Stål, *Talipes appendiculata* (da Fonseca), and

Hypsoprora coronata (Fabricius) all have large pits on the abdominal terga bearing a superficial resemblance to one another (Figs. 16, 18, and 20). However, the fine-structure

of these pits differs greatly: *G. tricorniger* (Fig. 17) has simple inornate pits, *T. appendiculata* (Fig. 19) has a single coeloconic sensillum in each pit, and *H. coronata* (Fig. 21) has a single papillose sensillum and three to five non-sensillar depressions per pit.

A trend in the evolution of subcellular protuberances is evident when representatives of the tribe Hoplophorionini (*sensu* Deitz 1975) are compared. In the genus *Ochropepla* (Fig. 22), for example, the protuberances are maximally developed as small acanthae, each bearing one or two acute projections. In the genus *Potnia* (Fig. 23), many of these acanthae are further divided into groups of three or more projections. The groups of microtrichia found in the genus *Alchisme* (Fig. 24) are each apparently homologous to a single acanthus of *Ochropepla*.

A similar trend occurs among the species of the genus *Aconophora*. The non-sensory protuberances of *Aconophora cultellata* Walker (Fig. 25) are maximally developed as single to tridentate acanthae. The acanthae of *Aconophora griseescens* (Germar) (Fig. 26) are multidentate. In a third (undescribed) species (Fig. 27), the acanthae each have several blunt crenulations, suggesting a secondary reduction of the pointed denticulae found in other species of the genus.

A more extensive survey of the integumental fine-structure of Auchenorrhyncha is needed to determine whether this previously overlooked complex of characters supports current taxonomic classifications of the group. Furthermore, elucidation of the functions of the sensilla described herein may provide valuable information concerning the evolution and ecology of the taxa in which they occur.

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